

# **Modeling Population and Ecosystem Response to Sublethal Toxicant Exposure**

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## **LONG TERM GOALS**

The ecological effects of environmental stress occur within complex communities and ecosystems. Prior to the current award, the PIs formulated and tested general dynamic energy budget models characterizing the response of individual organisms to toxicants, and developed methodology for using these models to predict population dynamics. They also developed new theory describing the trophic dynamics of open systems. They now propose to use these advances as the basis of research to test the predictive power and limitations of an individual-based approach to understanding the impact of pollutants on the dynamics of marine communities and ecosystems with multiple trophic levels.

## **OBJECTIVES**

The research has three main components:

- a) Models of the acclimation of individual organisms to changes in their environment.
- b) Development of simple models of marine organisms in open populations competing for a single resource in a polluted environment. Tests against data on estuarine fish experiencing environmental gradients.
- c) Development of simple ecosystem models with primary producers, competing herbivores and explicit incorporation of microbial dynamics. Tests of the models using experimental data on polluted benthic microcosms obtained by Dr. Kevin Carman (Louisiana State University). Use of the models to interpret field data on infauna near point sources of pollution.

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## APPROACH

Underpinning all the research are *dynamic energy budget* (DEB) models of individuals. We use simple DEB-based *individual-based models* to describe changes in structure and biomass of populations, with mechanistic descriptions of competition included where appropriate. We are developing ecosystem models that describe the flow of elemental matter in a way that is consistent with the DEB models of individuals.

### *Dynamic energy budget models*

Toxic compounds may reduce the fecundity, development rate, and/or survival probability of *individual organisms*. These changes can be modeled using dynamic energy budget (DEB) models incorporating information on the physiology of individuals (Kooijman 1993, 2000; Nisbet et al. 2000). DEB models describe the rates at which individual organisms assimilate and utilize energy from food for maintenance, growth, reproduction and development. These rates depend on the state of the organism (age, size, sex, nutritional status, etc.) and the state of its environment, (food density, temperature, toxicant levels, etc.). Solutions of the model equations represent the life history of individual organisms in a potentially variable environment.

### *Individual-based models of populations*

Individual based models (IBMs) treat a population as a collection of individuals, each growing, reproducing and dying in response to its physiological state and to the local environment. We use IBMs in which the physiology of individuals is described by a DEB model. Previous research on zooplankton dynamics (Nisbet et al. 1997), and related research on microbial populations (Kooijman 1993, 2000) has established that in a wide range of situations, we can successfully predict biomass changes using simple ordinary differential equations, derived by making special assumptions that simplify our DEB models. Where possible, such simplified descriptions are used in the current work.

### *Community dynamics: competition and mutualism*

The cornerstone of traditional ecological theory of competition is the competitive exclusion principle, which asserts that two or more species cannot coexist on a single resource. However, the scope of much of this theory is restricted by the assumption of “closed” populations, where recruits are the offspring of existing members of the population and the effects of immigration and emigration are negligible. We use recent competition theory for “open” benthic systems, originally developed through previous ONR funding (Wilson et al. 1999), and extended as part of the present research (Richards et al. 2000; see also report to ONR for FY 1999, 2000). This theory exploits the biomass-based approach described above, our criterion for two species to “coexist” being that each can grow in the presence of the other. This work was detailed in the report for FY2000, and during FY2001 we have extended the concepts to include mutualism (see below).

## *Modeling ecosystems*

In ecosystems, the state variables no longer relate to populations, but to functional groups of populations (e.g. decomposers, primary producers and herbivores) or to the chemical make-up of the constituent populations and the environment. The full potential of DEB models for marine ecosystem modeling remains an open issue, but existing models of the flow of energy and elements (e.g. Ross et al., 1993a; Gurney and Nisbet, 1998; chapter 7) make a convincing case that ecosystems do truly have dynamics that can be described by relatively simple, general, models. Our research exploits one important property of DEB-based ecosystem models: the capability to link the description of biological and chemical phenomena. The development of appropriate methodology is part of the on-going research (see section d below); as a starting point we use a model developed by Kooijman and Nisbet (2000) of mass and energy turnover in a closed ecosystem with primary producers, herbivores and decomposers. Individuals at each trophic level grow and reproduce in accordance with a DEB model. Assumptions on stoichiometry enable calculation of the fate of up to 16 compounds. Important quantities predicted include carbon dioxide production, oxygen consumption and ammonia production.

## **WORK COMPLETED**

Highlights of FY 00 include:

- New rigorous tests of toxicity models.
- Completion of study of models incorporating herbivore stoichiometry.
- New models of mutualism.

## **RESULTS**

### *New tests of toxicity models*

As noted above, toxicants in sublethal amounts may modify the energy budget of an organism. Common observations include less feeding activity and enhanced respiration in the presence of toxicants. We have modeled those toxic effects as effects on model parameters. Since there are several model parameters that can be potentially affected, we have investigated how we can distinguish among toxic effect mechanisms using artificial data. We previously concluded that using solely measurements on growth and reproduction, we can not easily distinguish between alternative toxic effect models. Thus in that previous work we assumed that toxicants reduce the feeding and assimilation rate of an organism as a hyperbolic function of the body burden of toxicant, and that the maintenance requirements of an organism increase linearly with the body burden,  $c$ , of contaminant:

$$A \rightarrow AX; \quad M \rightarrow M / X \quad \text{with} \quad X = \left( \frac{1}{1 + \frac{c - c_0}{K}} \right)$$

where  $c_0$  is the no effect concentration (NEC) and  $K$  is a constant characterizing the strength of the toxicant effect.

By contrast, Kooijman and co-workers (Kooijman 2000 and references therein), in a large project that used DEB models to estimate NECs, assumed that a single flux would be influenced at a lower level of contaminant than the others (analogous to the minimum rule in chemistry). The difference between models turns out to be of little importance for NEC estimation, but is likely to have substantial consequences for population dynamics (Gurney et al. 1996) and for ecosystem models (Kooijman and Nisbet 2000). We therefore tested the assumptions directly on several combinations of toxicant and organism, including previously reported examples of the effect of pentachlorophenol and tributyltin on the rates of feeding and respiration in the marine mussel *Mytilus edulis* (Donkin et al., 1989; Widdows and page 1993). The model fits both data sets well. Model alternatives that assume toxic effects on processes other than maintenance and assimilation cannot fit those data in a satisfactory way. Moreover, using maximum likelihood methods, we have found that allowing both toxic scaling parameters having different values does not significantly (99% level) improve the fits relative to having the same value for both parameters. We have drawn similar conclusions from other toxicant and organism combinations.

#### *Population Models with herbivore stoichiometry*

C:N and C:P ratios vary greatly in algae as a result of their capacity to store nutrients. There is typically much less variability in the stoichiometry of grazers; furthermore grazers commonly have carbon to nutrient ratios lower than that of photosynthesizing algae. A consequence is the possibility of nutrient limited control of grazer growth. Some simple models of this situation were modeled by Andersen (1997) in the context of phosphorus limitation of the growth of freshwater zooplankton. We have generalized this work, in simple models where the concept of the synthesizing unit (SU) described by Kooijman (2000) allows a mechanistic representation of multiple limitations. We formulated population models, and investigated conditions for the existence and stability of viable herbivore populations. We found that the viability of the herbivore population depends strongly on the details of assumptions regarding feeding, assimilation and maintenance. Recycling rates in one particularly simple model are in good agreement with data on freshwater zooplankters. Details are in Muller *et al.* (*in press*).

#### *Models of mutualism*

Initial attempts to describe theoretically the population dynamics of mutualism utilized modified Lotka-Volterra (L-V) competition equations in which the sign of the interspecific interaction term was changed from negative to positive. Unfortunately, although L-V models make reasonable predictions for competitive interactions, results of early L-V mutualism models indicated that mutualistic interactions were highly unstable. This led to speculation that obligate mutualisms should be confined to stable environments such as tropical rainforests. Despite early theoretical prediction, it has become clear over the past two decades that mutualisms are, in fact, not confined to extremely stable environments, nor are they uncommon. Furthermore, contaminants can impact mutualistic interactions (e.g. coral bleaching). Working with Andrew Thompson (a graduate student in the Schmitt lab), we have used variants of the formalism used in our previous competition studies to develop models of mutualism that incorporate realistic environmental-based carrying capacities, immigration, and a variety of physiological mechanisms.

## IMPACT/APPLICATIONS

Our DEB modeling work aims to unify theory describing the effects of environmental stress on diverse range of organisms. A key component is the emphasis on model testing; insight gained here will be applicable in other contexts. The work on mutualism complements our previous work on competing herbivores. The new ecosystem models will link our research to the large body of empirical and theoretical work on the cycling of elemental matter in stressed environments.

## TRANSITIONS

The research is not yet at a point to move from research into the Navy fleet or to industry. It has been used in a project related to off-shore oil production. Many of the modeling concepts developed in this research will be used in the in a large, multi-investigator project funded by EPA on new ecological indicators for wetlands. This work involves scientists from UC Davis and UC Santa Barbara.

## RELATED PROJECTS

PI Nisbet led, and co-PI Muller participated in a working group at the National Center for Ecological Analysis and Synthesis (NCEAS) on the theme "Population level effects of toxicants". The working group met twice in FY 2000.

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